On the Development and Morphology of the Leaves of Palms.

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CONTENTS.

	PAGE
I. Introduction	249
II. The Ontogeny of the Palm Leaf	251
1. The "Plicated" Limb	251
2. The Membrane ("Coiffe")	254
3. The Terminal "Gland"	255
4. The "Ligule" and "Dorsal Scale"	256
III. The Morphological Nature of the Palm Leaf	257
IV. Summary	260
Acknowledgments	261
List of Memoirs Cited	261

I. Introduction.

In series of previous memoirs* I have discussed the phyllode theory of the Monocotyledonous leaf, both in general and in relation to a number of special cases. In the present paper I propose to consider the Palms, with a view to determining whether their highly peculiar leaf structure is open to interpretation on the lines which have suggested themselves in the course of my study of other families, in which the leaves are less obviously anomalous.

The mature Palm leaf consists of a closed basal sheath (sometimes continued upwards into an ochrea), a leaf-stalk, and a limb, which may be of palmate or pinnate form; the "fan" and "feather" types of limb grade into one another, the distinction depending only on the degree of elongation of the median rachis. The Fan-palms differ from the Feather-palms in one further point on which great stress is sometimes laid—namely, that they bear small excrescences at the base of the limb. The outgrowth on the ventral side is the so-called ligule; less frequently a corresponding but smaller structure, known as the dorsal scale, occurs on the opposite side.

The morphological value of the various members which constitute the Palm leaf will be discussed in a later section of this paper (pp. 257–60).

It has long been known that the "compound" appearance of Palm leaves is the result of secondary changes, and that these leaves are thus not truly equivalent to the divided or compound leaves of Dicotyledons. Nearly

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* Arber, A. (1921), and earlier papers there cited.

a century ago, A. P. de Candolle* pointed out that the young leaves of Palms are entire, and that it is only subsequently that they become torn into thongs (" déchirées en lanières ") ; the segments are thus merely pseudo-lobes (" prétendus lobes "). De Candolle emphasises the fact that, though the idea of cutting (" découpure ") enters so largely into the technical language of leaf-description, it is only to the Palms that such terms can be applied with literal exactitude.

Subsequent workers have carried back our knowledge of Palm leaves to the earliest stages in their developmental history. Von Mohl,† Karsten,‡ and Trécul,§ in the middle years of the nineteenth century, followed the course of their entogeny, and attempted to trace the stages passed through by the leaf-rudiment between its origin and that curiously plicate phase which is succeeded by the ultimate subdivision into separate segments. About forty years later, the subject received renewed attention, principally from Eichler‖ and Naumann;¶ the work of Eichler remains, even to the present day, the standard account of the development of Palm leaves. More recently, Deinega** and Hirmer†† have returned to certain aspects of the question which the earlier workers had left in some obscurity.

A study of the literature shows that, though there is essential unanimity as to the manner in which the simple leaf-limb splits into its ultimate pseudo-compound form, there are, on the other hand, marked differences of opinion about the history of *that early developmental period which precedes the actual subdivision of the leaf.* All workers are agreed that, at an extremely early stage, the upper part of the leaf-rudiment shows a series of deep furrows alternating with ridges, which give it an apparently plicate form. But authorities differ as to the mechanism by which this plication is brought about. One school has maintained that there is actual *splitting* of the leaf-tissues (von Mohl, Trécul, Naumann), while others hold that only *folding* takes place (Karsten, Eichler, Deinega, Hirmer). The discussion of these conflicting views will be postponed until after I have described my own observations on the ontogeny of the Palm leaf.

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* Candolle, A. P. de (1827).

† Mohl, H. von (1845).

‡ Karsten, H. (1847).

§ Trécul, A. (1853).

‖ Eichler, A. W. (1885).

¶ Naumann, A. (1887).

** Deinega, V. (1898).

†† Hirmer, M. (1919); see this paper for further references.

II. The Ontogeny of the Palm Leaf.

1. *The "Plicated" Limb.*

In my study of the Palms I have not confined myself to genera whose leaf development has hitherto remained undescribed, but I have examined every example of which I could obtain material, because I found that, as my standpoint differed somewhat from that of previous workers, the existing descriptions did not settle the questions with which I was particularly concerned. I have followed the mode of development of the young leaves in representatives of four of the five sub-families of the Palms, but in the case of the fifth group—the anomalous Phytelephanteæ (*Nipa* and *Phytelephas*)—I regret that I have been unable to obtain material. Most of my observations relate to the ontogeny of the leaves of seedlings of various ages, because it is almost impossible, in this country, to procure many apical buds of fully developed Palms. The plumular leaves are generally of simpler form than the leaves of the mature plant, but there is no reason to suppose that they differ from them in any essential respect in the early stages of ontogeny.

The species which I have examined are distributed as follows among the different tribes:—

I. CORYPHINEÆ.		
	Phœniceæ	*Phœnix canariensis*, Hort., *P. dactylifera*, L., *P. Rivieri*, Hort.
	Sabaleæ	*Chamærops humilis*, L. *Pritchardia filifera*, Lind. *Rhapis humilis*, Blume. *Thrinax excelsa*, Lodd. *Trachycarpus* (*Chamærops*) *excelsus*, H. Wendl., T. (*C.*) *Fortunei*, H. Wendl.
II. BORASSINEÆ.		
	Borasseæ	*Latania Commersonii*, J. F. Gmel.
III. LEPIDOCARYINEÆ.		
	Calameæ	*Dæmonorops* (*Calamus*) *melanochætes*, Blume.
IV. CEROXYLINEÆ.		
	Arecineæ	*Areca sapida*, Soland. *Bentinckia nicobarica*, Becc. *Howea Belmoreana*, Becc. *Oreodoxa regia*, H. B. et K.
	Cocoineæ	*Cocos Romanzoffiana*, Cham.

I find that in all these species—Fan- and Feather-palms alike—the mechanism of development of the plicated or lamellated limb follows essentially the same lines. For the sake of brevity, I will limit myself to three cases as examples. In the Fan-palm, *Trachycarpus Fortunei* (fig. 1, A–F), the second plumular leaf, examined at a very young stage, was found to have at the base a closed sheathing region (fig. 1, A); this was succeeded by the petiole (fig. 1, B), an organ of roughly triangular outline with a concave upper surface. The petiole retained this characteristic form for a very short distance only (about 20μ), and then the lamellate structure was rapidly reached by the development of a series of grooves penetrating deeply into the leaf-stalk tissue between the vascular bundles (fig. 1, C–F). In fig. 1, E, I have numbered the grooves to show the order of their origin. The process of grooving is a very rapid one, the stages between fig. 1, B, and fig. 1, E, taking place within a distance of about 0·5 mm.

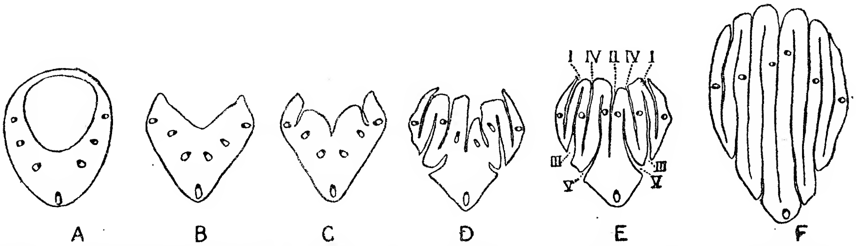

Fig. 1.—*Trachycarpus Fortunei*, H. Wendl. Series of transverse sections from below upwards through the second plumular leaf of seedling (×23). (Sections cut by Miss Ethel Sargant.) Fig. 1, A, sheath; fig. 1, B, petiole; fig. 1, C–E, process of invagination; fig. 1, F, final form. In fig. 1, E, the grooves are numbered in the order of their appearance. [Throughout figures—xylem represented black; phloem, white; fibres, dotted.] In this figure only principal bundles included.

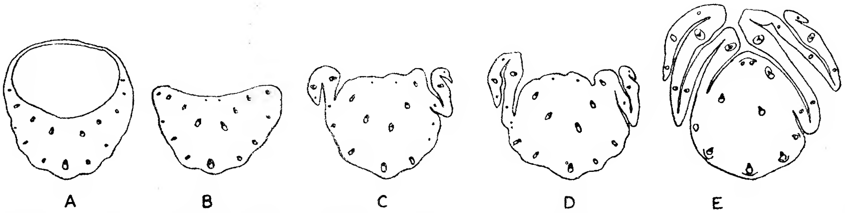

Fig. 2.—*Cocos Romanzoffiana*, Cham. Series of transverse sections from below upwards through second foliage leaf of seedling (×14). Fig. 2, A, sheath; fig. 2, B, petiole; fig. 2, C–E, stages in invagination.

That development proceeds on the same general principle in both Feather- and Fan-palms, is demonstrated by the comparison of fig. 1, A–F, with fig. 2, A–E, drawn from the second foliage leaf of *Cocos Romanzoffiana*. This series does not reach high enough into the leaf to show the final form of the limb, but it may be supplemented by reference to figs. 3, A–D, which were drawn from a set of sections cut from the third plumular leaf of another Feather-palm, *Oreodoxa regia*, H. B. et K. Fig. 3, A, shows an early stage in the grooving of the petiole; this section is interesting for comparison with the corresponding stages in the two Palms already considered, because the first grooves, in this case, are more or less parallel to the upper surface of the petiole, instead of being approximately at right angles to it.

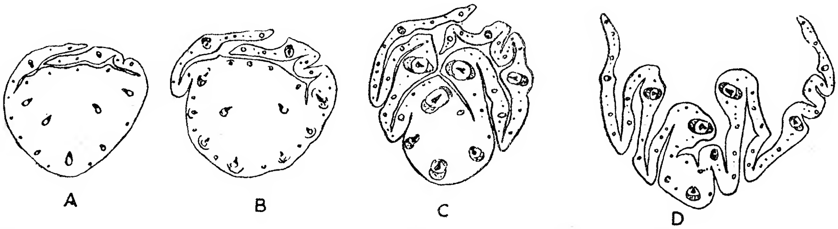

Fig. 3.—*Oreodoxa regia*, H. B. et K. Series of transverse sections through upper part of petiole, and limb, of third plumular leaf (first foliage leaf, which was preceded by two scale leaves) of seedling (×14); fig. 3, A, early stage of invagination of petiole.

As we have indicated on p. 250, two alternative explanations have hitherto been put forward to account for the resemblance of the young Palm leaf to a folded fan: (1) that there is a *splitting* of the tissues; and (2) that the rudimentary organ becomes *folded* in the course of development. I find it impossible to accept the first of these views, since my observations on the arrangement of the elements in the neighbourhood of the grooves entirely confirm the conclusion—already drawn by Hirmer* from a study of the detailed histology in certain genera—that no actual splitting takes place. But I am, on the other hand, unable to accept the second view, which Hirmer himself supports, namely, that the apparent plication is due to the folding of an originally simple leaf-rudiment (" Faltung der ursprünglich einfachen Blattanlage "). The word *folding* necessarily implies something which is the converse of the eventual unfolding of the blade. But no process takes place in the leaf-rudiment which can justly be described by such a term. I think it will be recognised that the way in which the grooves penetrate between the vascular strands, as shown in figs. 1–3, puts the folding hypothesis entirely out of court. My observations thus fail to support either the splitting or the folding interpretations; but they have led me to a third view, namely, *that the plications originate by invagination*, or, in other words, by differential growth in the course of which the outer cell-layers develop more rapidly than the inner tissues, and consequently, become wrinkled, or folded in, along certain lines. In relation to the epidermis alone, the word "folded" might perhaps be admissible, but the extension of the term to the leaf as a whole cannot be justified. It may possibly be thought that I am exaggerating the value of a slight distinction, in laying so much stress upon the difference between invagination and folding. But this distinction is by no means so trivial as it may appear at a casual glance, and I believe, moreover, that the impression conveyed by the description of the young Palm leaf as "folded" has been just sufficiently inexact to prevent botanists realising the true morphological nature of the leaves of Palms—a subject to which we shall return in a later section of this paper (p. 260).

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* Hirmer, M. (1919).

When we come to analyse the process of invagination more closely, we see that it must depend, in the last resort, on a tendency to disproportionate rapidity of growth in the surface layers as compared with those that are more deep-seated. And that such disparity should exist in the leaves is not surprising, when we realise that the Palms have undoubtedly a general tendency towards hypertrophy of the superficial tissues of their various organs. The results of this tendency are witnessed in the non-vascular spines which many Palms develop on the leaf-rachis, and in the squamiform ovarial hairs, which, in such cases as *Raphia Ruffia*, Mart., form eventually a woody coat to the fruit. The comparatively large size of the root-cap in the Palms may also be a case in point, for the calyptrogen, in the Monocotyledonous root, is the only tissue which is strictly epidermal. Possibly the integumental outgrowths, which ruminate the endosperm in many genera, may be regarded as another expression of the same tendency, while a further example is afforded by the proliferations producing the "coiffe" of the young leaf—a structure which we shall consider in the following paragraph.

2. *The Membrane* ("*Coiffe*").

It has long been known that the lamellæ of the very young leaves of certain Palms are connected by a kind of ephemeral membrane—the "Hülle," "Haut," "coiffe," or "pellicule"—so that the limb resembles a closed fan sheathed in tissue paper. This membrane is ruptured when the leaf unfolds. The view taken as to the nature of this envelope necessarily depends upon that held regarding the origin of the plications. To Von Mohl, Trécul and Naumann, the membrane was a primary constituent of the leaf, and represented the survival of the superficial tissues which were not involved in the splitting which these authors postulated. By those, on the other hand, who believe that the plications originate by folding, the membrane is held to be a secondary product, since it does not penetrate into the grooves. Deinega and Hirmer, who applied microtome technique to the problem of the origin of this membrane, conclude that it arises through secondary fusions occurring at the angles of the folds of the plicate leaf. My observations are entirely in harmony with this view, which was also indicated many years ago by Eichler. In some serial sections of the plumular leaves of *Trachycarpus Fortunei* and *Thrinax excelsa*, cut by Miss Ethel Sargant, I have been able to observe proliferated epidermal cells occluding the mouths of the invaginations (fig. 4, A–C). This occluding tissue no doubt represents the delicate early stage of the membrane which, later on, becomes so conspicuous a feature of the young leaf. The condition observed in these two genera thus confirms Hirmer's view, which was based on a study of another genus—*Phœnix*. It is much to be desired that some botanist, working at a tropical station where the leaves of a number of growing Palms are available, would give us a comprehensive account of the structure and history of the "coiffe."

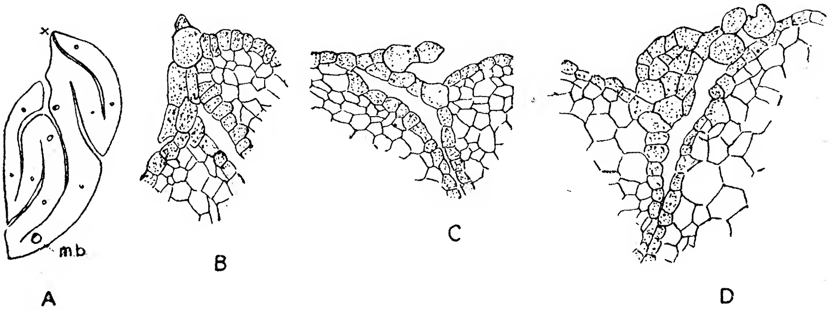

Fig. 4.—Epidermal proliferations in seedling leaves, from sections cut by Miss Ethel Sargant. Fig. 4, A–C, *Thrinax excelsa*, Lodd. Fig. 4, A, transverse section of third plumular leaf (× 47); *m.b.*, median bundle. Fig. 4, B, mouth of invagination marked × in fig. 4, A (× 318). The epidermis and its proliferation, which occludes the opening of the groove, are dotted. Fig, 4, C, another occluded groove, from lower down in the same leaf (× 318). Fig. 4, D, *Chamærops Fortunei*, Wendl. Mouth of invagination occluded by epidermal outgrowth, from a transverse section similar to that shown in fig. 1, F (× 318).

3. *The Terminal "Gland."*

Attention was drawn by Baillon* in 1895 to the fact that the first leaves produced by a Palm seedling are usually entire and parallel-nerved, and end in "une sorte de glande terminale, appareil excréteur, dont l'existence est passagère." I have observed this apical structure in the plumular leaves of *Phœnix dactylifera* (fig. 5, A–C) and *Pritchardia filifera* (fig. 5, D–F). In these cases the main part of the leaf-limb is, as usual, dorsiventral, whereas the apex is solid, and cylindrical in section (fig. 5, C and F). I have seen evidence of the glandular function which Baillon attributes to this apical region in

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* Baillon, H. (1895).

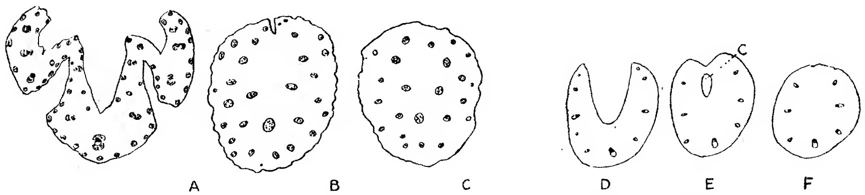

Fig. 5.—Solid tips of plumular leaves. Fig. 5, A–C, *Phœnix dactylifera*, L. Series of transverse sections from below upwards through apex of first foliage leaf to show dying out of invaginations (×14); bundles consist chiefly of fibres. Fig. 5, D–E, *Pritchardia filifera*, Lind. Series of transverse sections through apex of first foliage leaf (×14); fig. 5, E, shows that the apex is slightly hooded; *c*, cavity.

the case of *Bentinckia nicobarica*, where the tip of a plumular leaf bore conspicuous stomates and contained a plexus of tracheids. After cutting successive sections of the distal region of these leaves, I have come to the conclusion that the solid tip cannot be treated as if it were a separate organ, for it appears to owe its existence merely to the fact that the invaginations die out before they reach the distal end of the leaf. In *Pritchardia filifera* the solid apical part of the leaf is, as it were, slightly undercut by the termination of the median invagination, so that a minutely hooded apex is produced (fig. 5, E). The solid tips of the seedling leaves of *Pritchardia* and *Phœnix* seem to me exactly comparable with that of such a leaf as *Crocus*,* in which, also, the form of the apex is the result of the failure of the grooves to reach to the extreme end.

(4) *The "Ligule" and "Dorsal Scale."*

The origin of the outgrowths which occur at the base of the limb in the Fan-palms, and are commonly known as the "ligule" and "dorsal scale," cannot be studied satisfactorily in seedlings, since it is only in the later leaves that they arrive at their full development. The "dorsal scale" is seldom conspicuous, but the "ligule," though it is very variable in size and shape in different species, is often a striking object; fig. 6 shows its appearance in the case of the mature leaf of *Trachycarpus excelsus.* In order to follow the developmental history of these structures, I cut serial transverse sections through the apical bud of a well-grown shoot of *Rhapis humilis*. Fig. 7, A–D, represent the transition from stalk to limb in one of the young leaves of this bud. It will be seen that the invaginations, which are responsible for the

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* Arber, A. (1921), fig. 57, B, C, p. 324.

"plication" of the limb, fail, at their proximal limit, to reach the epidermis either on the ventral or dorsal side, so that part of the petiolar surface is, in each case, left overarching the base of the limb. This produces the "dorsal scale" at the back (fig. 7, B, *d.c.*), and the more prominent "ligule" on the ventral side (fig. 7, C, D, *v.c.*). The hooded tip of the plumular leaf of *Pritchardia filifera* (fig. 5, E) is a comparable case on a smaller scale, though here it is the distal end of the median invagination which is overarched by the ventral surface of the limb. I think it will be agreed that the almost cup-like form produced in *Trachycarpus excelsus* by the base of the limb and the "ligule" together (fig. 6), is consistent with the view that the "ligule" merely represents the limiting region of the uninvaginated proximal part of the petiole.

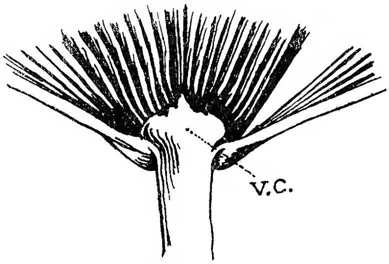

FIG. 6.—*Trachycarpus excelsus*, H. Wendl. Ventral view of junction of leaf-limb and petiole to show "ligule" or ventral crest, *v.c.* ($\times \frac{1}{2}$).

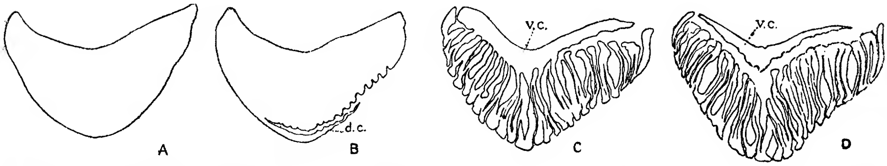

FIG. 7.—*Rhapis humulis*, Blume. Series of transverse sections through young leaf of mature plant, passing through junction of petiole and leaf-limb from below upwards (×9, circa); fig. 7, A, top of petiole; in fig. 7, B, invagination is just beginning and the slightly developed "dorsal scale" or dorsal crest (*d.c.*) is distinguishable; in fig. 7, C, the "ligule" or ventral crest (*v.c.*) is just becoming detached, while in fig. 7, D, it is entirely free. The asymmetry of fig. 7, B and C, is due to a slight obliquity in the series of sections.

The bearing of the interpretation of the "ligule" and "dorsal scale," which I have just outlined, upon the homologies of the Palm leaf, will be considered in the next section of this paper.

III. *The Morphological Nature of the Palm Leaf.*

There has never been any question among botanists as to the nature of the sheath which forms the extreme base of the Palm leaf; its homology with other leaf-sheaths is obvious. In certain Feather-palms (*Desmoncus, Calamus*) the apex of the sheath is continued upwards into the so-called ochrea, which clearly corresponds to the tubular ochrea of the Polygonaceæ, etc.

The sheath is succeeded by a stalk, for which I have throughout this paper used the word "petiole," but of which the homologies, at least in the case of the Fan-palms, are a matter of controversy. Domin* takes the view that the "ligule" of the Fan-palms is indeed a true ligule, corresponding to that of the Gramineæ, etc., and to the ochrea of the Rotangs; and since ligules are always defined as belonging to the leaf-sheath region, he draws the conclusion that in the Fan-palms the leaf-stalk, which comes below the "ligule," cannot be a true petiole, but must be of leaf-sheath nature. This view cannot but seem strained and artificial when one realises that it consigns the leaf-stalks of Fan- and certain Feather-palms to different morphological categories. Glück,† who also regards the ventral outgrowth as ligular, steers a middle course by treating it as the free apex of an extremely elongated ligule, which is fused with the petiole as far as the point of junction of stalk and limb. This speculation is ingenious, but, as I hope to show, unnecessary.

Both Domin's and Glück's views as to the nature of the "petiole" in the Fan-palms, stand or fall with the question of the homologies of the "ligule"—a problem which we must now consider. I should like to point out, in the first place, that it seems to me that any theory of the "ligule" must also take account of the corresponding structure which often occurs at the back of the leaf, and is known as the "dorsal scale." The latter is more variable than the "ligule," and though in some Fan-palms it is scarcely developed at all, I have observed in a Palm, grown under the name of *Sabal filamentosa*, that it may reach much the same degree of conspicuousness as the ventral structure. An inspection of the leaves of this Palm certainly suggests that no explanation of the origin of the "ligule" can be accepted which does not also embrace the "dorsal scale." But it is clear that the "dorsal scale" cannot be ligular, since no ligule is ever located *behind* the leaf to which it belongs, and it seems to me highly improbable that the ventral outgrowth should belong to a category from which the corresponding dorsal outgrowth is necessarily excluded.

In a preceding section of this paper I have discussed the ontogeny of the "ligule" and "dorsal scale," and the evidence there adduced has led me to the view that these structures have no more claim to be treated as distinct organs than have the solid apice of the plumular leaves described on pp. 255–6. The invaginations of the limb, in their proximal region, burrow as it were, under the ventral surface of the petiole, and to a much slighter extent, under the dorsal surface; on the ventral side the penthouse thus produced happens to be a striking object to the eye, and it may possibly become still more noticeable by suffering some further elongation after the invagination of the limb is completed, but these are not reasons which can entitle it to rank as a morphological entity. The conclusion I have reached is that the "ligule" and "dorsal scale" belong to the petiole, and are merely the outcome of the peculiar mode of limb-development characteristic of the Fan-palms. The appearance of these structures in the Fan-palms, and their absence in the Feather-palms, is due to the fact that in the Fan-palms the whole series of invaginations start from the same level, whereas, in the Feather-palms, where the plications occur to right and left of the median rachis, there is no crowding together of the invaginations at a single point.

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* Domin, K. (1911).

† Glück, H. (1901).

My view of the morphology of the "ligule" and "dorsal scale" leads me to suggest that these terms should be dropped, since the structures in question have nothing to do either with ligules or with scale-leaves; the term ligule will then be left for the tubular ochrea of *Desmoncus*, etc., to which it rightfully belongs. The best substitutes seem to be "ventral crest" and "dorsal crest," expressions based upon the word "Crista," already used by Drude* for the "ligule." If my interpretation of these structures be accepted, it leads inevitably to the conclusion that the leaf-stalk, both of the Fan- and Feather-palms, is the basal part of a true petiole.

And now, finally, we have to consider the nature of the leaf-limb. Strikingly different in aspect as are the mature blades of typical Fan- and Feather-palms, there is not, morphologically, any impassable gulf between the two types. If the median rachis is short or non-existent, we get the "fan" form, while, if there be long-continued growth, the "feather" leaf is produced; the leaves of such a genus as *Licuala*† show transitional characters. It seems possible that the "fan" type is the older, since the palmate form predominates among fossil Palms, while the Feather-palms are in the majority at the present day.‡ But the relative age of the two types must at present be treated as an open question, since they were both apparently in existence in the Upper Cretaceous. The evolution of the "feather" from the "fan" (or *vice versâ*) must have occurred more than once in the history of the family, since both types may be found among Palms which are regarded by systematists as allied. The sub-family Coryphoideæ, for instance, includes two tribes—the Phœniceæ, which are feather-leaved, and the Sabaleæ, which are fan-leaved; in the Lepidocaryineæ, again, there are two tribes differing in the same character—the fan-leaved Mauriteæ and the feather-leaved Metroxyleæ. These considerations seem to show that the various types of Palm leaf may safely be treated as homologous, whether they assume the palmate or the pinnate form.

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* Drude, O. (1889).

† Wendland, H. (1879).

‡ Unger, in Martius, K. F. P. von (1823–50).

As I have shown on pp. 251–4, the plicate limb, both in the Fan- and Feather-palms, is not, as has hitherto been commonly assumed, the result of the folding of a flat leaf-blade; it takes its origin, on the contrary, from the upper region of the leaf-stalk, through a series of invaginations which penetrate the tissues of this organ, and elaborate its more or less radial structure into a flattened and perfectly dorsiventral limb. My observations on the ontogeny thus indicate that the Palm leaf is not, as has been generally supposed, an organ whose structure is almost without a parallel, but that it falls into line with the leaves of other Monocotyledons (*e.g.*, certain Irids).*

I thus regard the Palm leaf, as a whole, as a petiolar phyllode, and its blade as a pseudo-lamina, analogous to, but not homologous with, the blade of a Dicotyledon. The fundamental identity of the leaf of the Palms with that of other Monocotyledons is, however, soon masked by secondary fusions, and, a little later, by the disintegration and tearing into segments, which the leaf undergoes in passing to its peculiar definitive form.

IV. SUMMARY.

The evidence from ontogeny and comparative morphology, brought forward in the present paper, leads to the following conclusions:—

1. The leaf-stalk, which succeeds the basal sheath, is, both in the Fan- and Feather-palms, the basal or proximal region of the true petiole.

2. The "fan" or "feather" limb is not, morphologically, a lamina, but is a modification of the distal region of the true petiole. The complex plication of the limb arises through the development of a series of invaginations which penetrate into the leaf-stalk tissue between the bundles.

3. The "ligule" and "dorsal scale" of the Fan-palms are not morphological entities, but merely represent the adaxial and abaxial distal margins of the uninvaginated proximal region of the petiole. The terms "ventral crest" and "dorsal crest" are proposed as substitutes for the terms "ligule" and "dorsal scale."

4. The Palm leaf, regarded as a whole, is, on the present interpretation, a petiolar phyllode with a pseudo-lamina—a conception which brings it into essential relation with the leaves of other Monocotyledons.

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* Arber, A. (1921).

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